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Sheep and goat preference for and nutritional value of Mediterranean maquis shrubs

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Abstract

The objective of this study was to evaluate the nutritive value, intake and preferences of sheep and goats for the dominant six shrubs of the holly oak maquis-type shrublands in Croatia. The experimental sheep ($n = 12$, mean weight 28.5 kg) were a local Croatian mixed breed. The experimental goats ($n = 12$, mean weight 13.4 kg) were a mixture of domestic goats crossed with Saanen and Alpine breeds. Sheep and goats differed ($P < 0.01$) in consumption of almost all of the shrubs. Goats had higher intakes (g/kg B.W., $P < 0.01$) than sheep of each shrub except *Quercus ilex*. In Trial 1, shrub intake for goats ranged from 17.7 ± 0.72 g/kg B.W. for *Pistacia lentiscus* to 33.1 ± 1.40 g/kg B.W. for *Erica multiflora*. Goats ate more *Arbutus unedo* ($P = 0.004$; 19.9 g/kg versus 14.2 g/kg B.W., respectively); *E. multiflora* (33.1 g/kg versus 21.9 g/kg B.W., respectively) and *Pistacia lenticus* (17.2 g/kg versus 10.6 g/kg B.W., respectively) than did sheep. Goats ate twice as much *Juniperus phoeniceae* ($P = 0.002$) as did sheep (21.0 g/kg versus 10.9 g/kg B.W.), and also ate more *Viburnum tinus* ($P = 0.02$) than did sheep (22.6 g/kg versus 13.9 g/kg B.W.). There was a day × treatment interaction ($P = 0.001$), with goats eating more *A. unedo*, *E. multiflora*, *J. phoeniceae*, *P. lenticus* and *V. tinus* than sheep. In Trial 2, the rank order of preference (highest to least) for goats were *Q. ilex*, *E. multiflora*, *V. tinus*, *A. unedo*, *J. phoeniceae* and *P. lentiscus*. The rank order by sheep was similar: *Q. ilex*, *E. multiflora*, *V. tinus*, *J. phoeniceae*, *P. lentiscus* and *A. unedo*. Overall, goats ate 50.5 g/kg B.W. of shrubs per day, while sheep averaged 26.7 g/kg B.W. each day. Goats are better suited to graze Mediterranean maquis in terms of potential shrub use.

Keywords: Mediterranean maquis; Sheep; Goats; Shrub preference; Nutritional value

1. Introduction

Mediterranean vegetation commonly known by the French terms “maquis” (i.e., woody plants < 5 m tall) and “garrigue” (i.e., chaparral, dominated by ≤1 m

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tall shrubs) are two main types of shrubby vegetation on degraded soils in northern Mediterranean countries (Horvatić, 1957). Together these types of vegetation cover over 1 million ha in the Mediterranean area of Croatia (Rogosic et al., 2003) and about 100 million ha in the countries around the Mediterranean basin (Le Houerou, 1981).

These shrublands are a critical source of forage for livestock, with sheep and goat production comprising 60–80% of the total agricultural output in this region. Rainfall is more than adequate (800–1200 mm annually), and browse production is typically near 1000 kg DM/(ha year) (Rogosic, 2000). With more intensive management, including concentrated grazing, periodic harvest of shrubs, and fertilization, browse production can be increased 4–6 times (Long et al., 1978).

Maquis dominated by holly oak (*Quercus ilex*) are dense and nearly impassable evergreen thickets about 3 m high. The dominant shrub species are generally of low nutritional quality and contain secondary metabolites, such as tannins, terpenes and volatile oils (Tisserand and Alibes, 1989; Van Soest, 1994; Bartolomé et al., 1998). Nonetheless, these shrubs are often selected by grazing animals, because their leaves have more protein and less fiber than leaves and stems of grasses (Holechek et al., 1989; Papachristou and Nastis, 1990). Thus, grazing by sheep, goats or donkeys can provide important source of forage for small-scale landowners (Devendra, 1990). The objectives of this study were to evaluate the nutritive value, intake and preferences of sheep and goats for key shrubs of the holly oak (*Q. ilex*) maquis plant community in Croatia. This information is an important first step toward better utilization and management of these grazing resources by sheep and goats in Croatia and the Mediterranean Region.

2. Materials and methods

2.1. Study site

The experiments were conducted during summer (June–July, 2000) and fall (September–October, 2000) on a private farm on the island of Brac, 5 km from the Croatian coastal city of Split (43°22′N; 16°38′E). The island has a Mediterranean climate, with an average annual temperature of 16.5 °C and average annual rainfall of about 950 mm (Split Meteorological Station; 10 year mean). It is dry from June to September and moderately wet during the rest of the year. The research farm was situated in an area with holly oak maquis on the northern end of the island. In Croatia, maquis vegetation is widespread on the deep red soils termed "terra rossa." In total, there are about 60 plant species represented in the holly oak maquis vegetation on this island (Rogosic, 2000), dominated by low trees and shrubs, with some dwarf shrubs mixed with perennial grasses and numerous forb species.

2.2. Study shrubs and animals

We studied six shrubs: *Q. ilex* L. (Cupuliferae), *Erica multiflora* L. (Ericaceae), *Arbutus unedo* L. (Ericaceae), *Juniperus phoeniceae* L. (Pinaceae), *Viburnum tinus* L. (Caprifoliaceae) and *Pistacia lentiscus* L. (Anacardiaceae). They are all evergreen, so their twigs and leaves are available year-round. Together they constitute 70% of the shrubby vegetation from amongst a total of browse species occurring in this vegetation type (Rogosic, 1995). They are all important dietary components for sheep and goats (Rogosic and Knezevic, 1994).

The experimental sheep, 5-month-old ($n = 12$, mean weight 28.5 kg) were a local breed that is a cross between the Croatian breeds "Pramenka" and "Wunterberg." In general, the characteristics of the Pramenka sheep are low production, slender body conformation and sparse, low-quality wool. Even so, the Pramenka breed is adapted to the local ecological conditions in the Croatian littoral and they are particularly adept at grazing shrub ranges. The experimental goats, 2.5-month-old ($n = 12$, mean weight 13.4 kg), were a mixture of domestic goats crossed with Saanen and Alpine breeds. These goats are noted for milk production and excellent foraging capabilities on shrub ranges in the Adriatic region. Each group of experimental animals had an approximately equal mix of both sexes. All animals were raised on the same farm on the island of Brac (Central Dalmatia) utilizing the shrubby vegetation of the Mediterranean maquis. Both the sheep and goats were weaned at 7–8 weeks of age, as is typical in this region for lactating females. All animals were experienced at browsing on the native vegetation, as the kids and lambs ate some shrubs even while nursing, and after weaning most of their diets consisted of shrubs.

2.2.1. Trial 1. Preference for shrubs fed individually

All animals were penned individually, with water and trace mineral salt provided free-choice. Pens (2 m × 3 m) were outdoors, and made of metal mesh wire, with concrete floor and canvas shade cloth above. An initial adaptation period of 7 days was used to accustom the animals to the pen conditions. Baseline intake of alfalfa pellets was determined for each animal on days 1–5, and they were offered each shrub individually for 10 days. These 10-day periods were sufficient to determine shrub intake because these animals were raised on these shrub ranges from last 3 weeks. The study was conducted during June, July, and August 2000. Initially, *A. unedo* was fed from days 6 to 15, then baseline was re-established using alfalfa pellets (days 16–18). The other five shrubs were fed in a predetermined order with a baseline period between feeding trials. The baseline feeding period was used to determine if environmental conditions altered intakes over time. For each shrub, the leaves and current season's growth twigs were harvested with clippers early in the morning, and then freshly harvested material was ground through a 1 cm screen. Ground material was mixed for uniformity and offered fresh to individual animals ad libitum from 08:00 to 14:00 h daily for 10 days; refusals were collected and weighed daily at 14:00 h. Animals were given a supplement of 100 g ground barley daily during the experiment after refused shrubs were weighed. Ground barley contained 8.1% CP, and provided 3.43 Mcal of ME/kg for small ruminants (Kearl, 1982). The daily ME requirement for Mediterranean sheep and goats of these sizes is approximately 1.6 and 1.0 Mcal, respectively (Kearl, 1982); thus, the barley supplement provided approximately 21 and 34% of the daily ME requirements for sheep and goats, respectively. Animals were weighed at the beginning and end of shrub feeding.

2.2.2. Trial 2. Preference for shrubs offered jointly

After the individual shrub pen trials, acceptability of the six shrubs offered jointly, but in separate boxes was determined using another set of similar animals at the same location on the island of Brac. Age and breeds were the same as previously described for Trial 1; groups were an equal mix of male and female. Sheep ($n = 6$) weighed 27.3 kg at the beginning trial and 24.8 kg at the end of trial, while goats ($n = 6$) weighed 14.5 kg at the beginning and 14.2 kg at the end of the trial. The study was conducted during September–October, 2000. Six lambs and six kids were fasted overnight, then trained for 4 days to eat from six food boxes in six locations in their pen each morning using a small amount of grain in each food box. After training (i.e., all animals learned to eat from all boxes), a 6-day trial was conducted. Each day, animals were given a 100 g preload of ground barley at 08:00 h, then at 08:30 h freshly harvested and ground shrubs were placed in each of the six boxes. Additional shrub material was added as necessary every 30 min until 14:00 h. Feed refusals were collected and intake of each shrub was calculated. Each day the shrubs were rotated to another position during the 6-day trial.

2.3. Collection and chemical analysis of plant material

Leaves and current season's growth (up to 5 cm length) twigs of each shrub were harvested for nutritional analysis. Daily samples of each shrub were weighed, dried at ambient temperature, and ground to pass a 1-mm screen in a Willey mill, and a weekly composite of these was used for chemical analysis. All analyses were carried out on duplicate samples and results reported on DM basis. The DM content of shrubs was determined by oven drying at 105 °C for 24 h, and ash was determined by ashing samples in a muffle furnace at 600 °C for 16 h (AOAC, 1990). Ether extract (EE) was extracted with petroleum ether (40–60 BP) on a Soxtec System 1040 Extraction Unit (FOSS Tecator AB, Sweden) and CP (Nx6.25) was determined by the Kjeldahl method (AOAC, 1990) on a Kjeltec 2200 Auto Distillation system (FOSS Tecator AB, Sweden). The method of Henneberg and Stohmann (1859) was used to determine crude fiber (CF). Neutral detergent fiber (NDF, with Na-sulfite added without alpha amylase), ADF and acid detergent lignin (ADL) determinations were done according to Robertson and Van Soest (1981). All fiber fractions were analyzed on a Fibertec 1030 Hot Extractor (Tecator, Sweden). Non- fibrous carbohydrate (NFC) was calculated by difference:

$$\text{NFC} = 100 - (\%\text{NDF} + \%\text{CP} + \%\text{EE} + \%\text{Ash})$$

(NRC, 2001).

Phosphorus was determined by a colorimetric method (Cawell, 1955). Samples were analyzed for in vitro organic matter digestibility (IVOMD) using the cellulose–pepsin method (Aufrère, 1982). This technique involved two stages: (1) pre-treatment with pepsin (pepsin Merck no. 7190; 1:10,000) in hydrochloric acid (0.2% pepsin in 1N HCl) in a water bath at 40 °C for 24 h; (2) digestion by cellulase (cellulase Onozuka R 10 extracted from *Trichoderma viride*, Yakult Honshoa Co., Ltd., Japan) after filtration and rinsing, for 24 h in a water bath at 40 °C. Digestibility of energy (DE) of shrubs was related to IVOMD by the following equation for untreated and treated straw: DE = 0.985OMD (%) − 2.95 (INRA, 1989). Digestible, metabolizable and net energy for lactation (DE, ME and NEL, respectively) were calculated from chemical analyses, without ether extract and DE (%) data according to the method of INRA (1989). Shrubs were also analyzed for tannins using colorimetric methods described by Waterman and Mole (1994). Tannin concentrations are expressed as a relative tannin index.

2.4. Statistical analysis

The experimental design for the shrubs fed individually to sheep and goats was a completely random design with a separate analysis for each shrub. The model included treatment (i.e., sheep versus goats), with individual animals nested within treatments, and repeated measures over the 10-day trial. Animals were a random factor in the mixed model analysis (SAS, 2000).

Six sheep and six goats were used in separate trials to assess acceptability of the six shrubs fed in a cafeteria-style arrangement within their individual pen. This series of trials used a Latin square design with each animal comprising an individual square. The model was animal in pen (i.e., square), position in pen, day in pen, plant species (i.e., treatment), and error (Pfister et al., 1996). The protected LSD procedure was used to compare individual means (SAS, 2000). All analyses on shrub intake were adjusted for body weight (g/kg B.W.).

3. Results

3.1. Nutritional composition

The nutritional composition of the six shrubs varied considerably (Table 1). Overall, the CP content of all shrub leaves + twigs was low (mean 6.4%) and ranged from 4.9% (*E. multiflora*) to 7.8% (*P. lentiscus*).

Table 1
Chemical composition (mean ± S.D., DM basis) of six Mediterranean shrub species fed to Croatian sheep and goats

Species	*Arbutus unedo*	*Quercus ilex*	*Juniperus phoeniceae*	*Erica multiflora*	*Pistacia lentiscus*	*Viburnum tinus*	Average
Dry matter	49.8 ± 2.0	61.4 ± 1.7	54.7 ± 1.4	48.9 ± 1.3	51.0 ± 1.2	46.9 ± 1.1	52.1 ± 1.3
Ash	4.2 ± 0.27	4.3 ± 0.25	5.3 ± 0.26	2.7 ± 0.17	6.2 ± 0.39	5.6 ± 0.36	4.7 ± 0.28
Crude protein	5.6 ± 0.34	7.4 ± 0.40	5.6 ± 0.37	4.9 ± 0.22	7.8 ± 0.50	7.2 ± 048	6.4 ± 0.39
Ether extract	6.3 ± 0.35	3.3 ± 0.16	8.9 ± 0.45	8.6 ± 0.48	3.2 ± 0.15	9.4 ± 0.38	6.6 ± 0.33
Crude fiber	16.8 ± 1.68	30.4 ± 2.58	28.4 ± 2.27	38.8 ± 3.50	18.23 ± 1.58	20.3 ± 2.2	25.6 ± 2.3
NDF	46.7 ± 5.60	62.6 ± 6.31	53.9 ± 5.23	62.9 ± 5.66	53.0 ± 4.72	53.4 ± 6.28	55.4 ± 5.63
ADF	37.2 ± 3.16	47.3 ± 3.55	41.0 ± 3.61	51.8 ± 4.39	31.1 ± 2.64	37.7 ± 2.86	41.0 ± 3.37
ADL	24.0 ± 3.35	24.5 ± 3.94	24.1 ± 1.93	33.0 ± 1.89	17.9 ± 1.86	22.1 ± 1.26	24.3 ± 2.37
ADL/ADF	51.34	39.09	44.85	52.50	33.77	41.27	43.80
NFC	37.6 ± 4.47	24.5 ± 1.96	26.2 ± 2.24	30.0 ± 3.18	29.7 ± 3.28	24.5 ± 2.9	26.8 ± 3.0
IVOMD	43.0 ± 2.58	35.7 ± 2.49	35.5 ± 2.84	27.2 ± 1.77	32.2 ± 2.57	43.4 ± 2.6	36.2 ± 2.48
Energy value							
ME (MJ/kg DM)	6.54 ± 0.37	5.4 ± 0.32	5.38 ± 0.24	4.14 ± 0.23	4.84 ± 0.28	6.57 ± 0.41	5.27 ± 0.31
NEL (MJ/kg DM)	4.33 ± 0.24	3.57 ± 0.21	3.56 ± 0.16	2.74 ± 0.15	3.21 ± 0.19	4.35 ± 0.27	3.49 ± 0.21
Ca	1.47 ± 0.18	1.43 ± 0.13	2.04 ± 0.22	0.4 ± 0.3	1.59 ± 0.19	1.30 ± 0.12	1.36 ± 0.15
P	0.08 ± 0.01	0.07 ± 0.01	0.09 ± 0.01	0.06 ± 0.01	0.10 ± 0.01	0.09 ± 0.01	0.08 ± 0.01
Ca/P	18.38	20.43	22.6	7.50	15.90	14.44	16.55
Tannin index	1.33	0.99	0.86	0.98	1.48	-	1.08

The shrub samples had high moisture content (mean 48%), perhaps because waxy leaf surfaces (part of ether extract) protect against intense summer UV radiation. Shrubs had high concentrations of cell wall constituents (NDF and ADF), particularly lignin (ADL). ADL (sum of lignin, cutin and detergent insoluble minerals) was a major part of cell wall constituents and contributed to the 44% ADF value. The high tannin indices for *P. lentiscus* (1.48), *A. unedo* (1.33), *E. multiflora* (0.98), *Q. ilex* (0.99) and *J. phoeniceae* (0.86) indicate high tannin concentrations. There were negative correlations between goat intake ($r = -0.61$), sheep ($r = -0.45$) and tannin content in the investigated shrubs. *E. multiflora* was highest in CF, NDF, ADF and ADL, and lowest in CP, ME, IVOMD and NEL. In contrast, *A. unedo* had the lowest level of cell wall carbohydrates and the highest NFC concentration, and consequently higher IVOMD and NEL values. Digestibility coefficients were highest for *V. tinus* and *A. unedo* (43.4 and 43.3%, respectively). *Q. ilex*, *J. phoeniceae* and *P. lentiscus* (35.7, 35.5 and 32.2%, respectively) were intermediate in digestibility, whereas *E. multiflora* was highly indigestible (27.2%).

All shrubs exhibited high (mean = 1.36%) but variable Ca concentrations (range = 0.45–2.04%), and Ca/P ratios (mean = 16.55; range = 7.50–22.6), except *E. multiflora*. All shrubs also had very low (mean = 0.08%), but uniform P levels.

3.2. Trial 1. Preference study

3.2.1. Sheep versus goats

Sheep and goats differed in consumption of almost all of the shrubs (Table 3). Goats had higher intakes than sheep (g/kg B.W., $P < 0.01$) for all shrubs except *Q. ilex*. The average intake by goats of all shrubs was 22.1 g/kg B.W., while that for sheep was 14.2 g/kg B.W. In all cases except for *Q. ilex*, there was a day effect and a day × treatment interaction ($P < 0.05$) as goats and sheep generally did not differ in shrub intake on day 1 or 2, but goats ate more than sheep as the trials progressed (Fig. 1).

3.2.2. Preferences for individual shrubs

Goats ate more *A. unedo* ($P = 0.004$) than did sheep (19.9 g/kg versus 14.2 g/kg B.W., respectively) (Table 2). There was a day × treatment interaction ($P = 0.001$), with goats eating more *A. unedo* on days 5 and 8–10 (Fig. 1). Similarly, goats ate more *E. multiflora* ($P = 0.0004$) than did sheep (33.1 g/kg versus 21.9 g/kg B.W., respectively). Also, there was a day × treatment interaction ($P = 0002$), with goats eating more *E. multiflora* on some days than did sheep, but there were no significant differences on days 1, 5, 7 and 8 (Fig. 1). Goats ate twice as much *J. phoeniceae* ($P = 0.002$) as did sheep (21.0 g/kg versus 10.9 g/kg B.W.). There was significant day × treatment interaction ($P = 0.02$) for *Juniperus* consumption, since goats ate more *J. phoeniceae* than did sheep on all days except for days 1 and 6 (Fig. 1). Goats ate more *Pistacia lenticus* ($P = 0.004$) than did sheep (17.2 g/kg versus 10.6 g/kg B.W.), except on days 1 and 5, which caused a day × treatment interaction ($P = 0.0001$) (Fig. 1). Goats also ate more *V. tinus* ($P = 0.02$) than did sheep (22.6 g/kg versus 13.9 g/kg B.W.), except on days 1 and 2, which resulted in a day × treatment interaction ($P = 0.03$), (Fig. 1). Goats and sheep did not differ ($P = 0.24$) in intake of *Q. ilex* (15.9 ± 0.8 g/kg B.W.). There was a day effect ($P = 0.0001$) as both goats and sheep increased intake from the first to the last day of the trial (Fig. 1).

Table 2
Daily intake (fresh weight; g/kg B.W.) of six Mediterranean browse species offered individually to Croatian sheep and goats (average of 10 days)

Shrub species	Animals		
	Goats	Sheep	P[a]
	Mean ± S.E. (g/kg B.W.)		
Arbutus unedo	19.9 ± 0.76	14.2 ± 0.46	0.004
Erica multiflora	33.1 ± 1.4	21.9 ± 0.56	0.0004
Juniperus phoeniceae	21.0 ± 1.0	10.9 ± 0.73	0.002
Pistacia lentiscus	17.7 ± 0.72	10.6 ± 0.39	0.004
Quercus ilex	18.3 ± 1.35	13.6 ± 0.82	0.24
Viburnum tinus	22.6 ± 1.11	13.9 ± 0.64	0.02

[a] Observed significance level for comparison of goats vs. sheep.

3.3. Trial 2. Latin square preference study

There were marked differences in intake of shrubs by goats ($P = 0.0001$; Table 3). Goats preferred *Q. ilex* and *E. multiflora* ($P < 0.05$) over all other shrubs; they also preferred *V. tinus* over *A. unedo*, *J. phoeniceae* and *P. lentiscus* ($P < 0.05$). The preference for the shrubs in rank order was (greatest to least): *Q. ilex*, *E. multiflora*, *V. tinus*, *A. unedo*, *J. phoeniceae* and *P. lentiscus*.

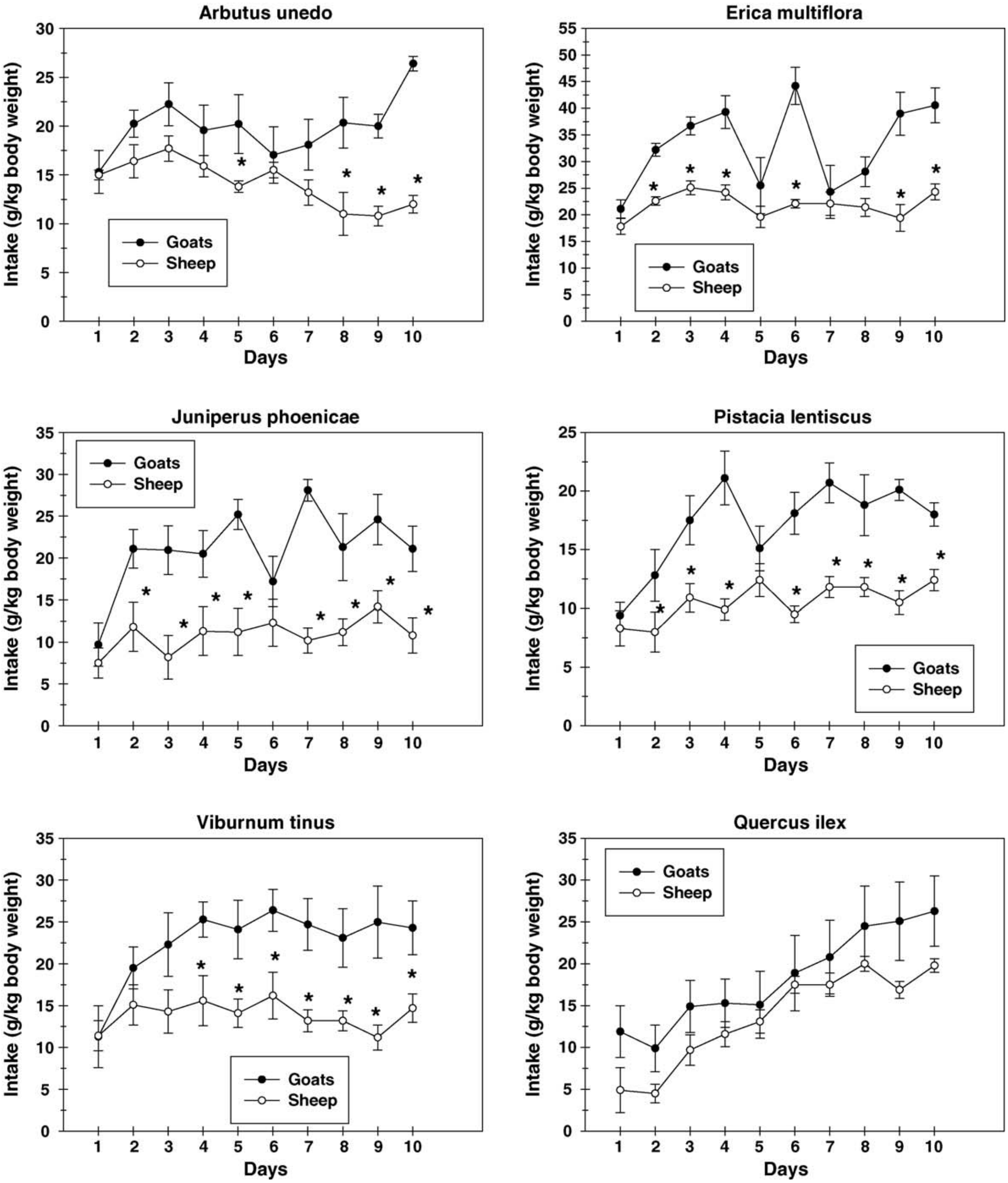

Fig. 1. Intake of individual shrubs by goats and sheep over 10-day trial periods. Asterisks indicate ($P < 0.05$) differences on a specific day between goats and sheep.

Table 3
Daily intake (g/kg B.W.) of six Mediterranean browse species offered simultaneously to Croatian sheep and goats (average of 6 days)

Shrub species	Animals	
	Goats	Sheep
	Mean ± S.E. (g/kg B.W.)	
Quercus ilex	15.0 ± 0.88^{a}	11.0 ± 0.48^{a}
Erica multiflora	13.7 ± 0.77^{a}	6.7 ± 0.52^{b}
Viburnum tinus	10.1 ± 0.95^{b}	5.1 ± 0.63^{c}
Arbutus unedo	4.3 ± 0.56^{c}	1.2 ± 0.25^{d}
Juniperus phoeniceae	4.2 ± 0.77^{c}	1.4 ± 0.25^{d}
Pistacia lentiscus	3.2 ± 0.75^{c}	1.3 ± 0.24^{d}

$^{a-d}$Means in the same column with a different superscript differ ($P < 0.05$). All shrub values are fresh weights.

Sheep exhibited similar preferences, as did goats ($P = 0.0001$; Table 3). Sheep differed ($P < 0.05$) in consumption of *Q. ilex*, *E. multiflora* and *V. tinus*, which were all more preferred than the other three shrubs (Table 3). Rank order of preference by sheep was *Q. ilex*, *E. multiflora*, *V. tinus*, *J. phoeniceae*, *P. lentiscus* and *A. unedo*. This trial did not directly compare sheep and goats, but numerically goats ate about 25–75% more of each shrub than did sheep. Overall, goats ate 50.5 g/kg B.W. of shrubs per day, while sheep averaged 26.7 g/kg B.W. each day.

4. Discussion

4.1. Chemical composition of the major holly oak maquis shrubs

The chemical composition of these Mediterranean maquis shrub species is likely to have a major impact on consumption by goats and sheep (Bryant et al., 1991). The six studied shrubs are generally considered to be of low to intermediate nutritional quality because they contain less than 55% digestible OM, 8% CP and 10% soluble sugars and starches (Leng, 1990). They also contain volatile oils and secondary compounds, such as tannins, that can reduce nutrient availability (Thomson et al., 1987).

Protein content was lowest and fiber highest in shrubs during summer (Rogosic and Dumancic, 1996). Shrubs had levels of protein (4.89–7.82% in DM) in the range (6–8%) below which recycling N does not satisfy requirements of rumen microbes resulting in decreased forage digestibility and intake (Van Soest, 1994). Dry matter intake is influenced to a large extent by dietary CP content. A sharp decline in intake occurs when forages contain less than 7% CP (Milford and Minson, 1965). Micro-organisms fermenting structural carbohydrates (NDF) require only ammonia as their N source (Russell et al., 1992), and the minimum level of rumen fluid ammonia for optimum voluntary intake of low-N, low-digestibility forage by cattle is about 200 mg NH_3-N/l, even though the digestibility of the forage (in nylon bags) was optimized below 100 mg NH_3-N/l (Krebs and Leng, 1984; Perdock et al., 1986). The fiber content of forages varies greatly depending on environment, stage of maturity and leaf/twig ratios (Buxton and Fales, 1994). High temperatures and solar radiation increase fiber fractions because of thickened cell walls (Wilson et al., 1991) and enhanced lignin synthesis, both of which lower digestibility (Buxton and Fales, 1994). Lignin limits the availability of plant cell walls to ruminants and to rumen microbes (Van Soest, 1994), but it does not influence the digestibility of CP and other non-cell wall components.

Average tannins (1.08%) contained in investigated shrubs can reduce intake and digestibility of forage by sheep and goats (Butler, 1989). Depending on their structure and concentrations, tannins can have adverse or beneficial effects on forage digestibility and intake. Some tannin reduce digestibility of protein, whereas others are toxic. Condensed tannins are found in 80% of the Mediterranean vascular plants (Silanikove et al., 1994). At low concentrations, some condensed tannins can improve nutrition for ruminants by reducing protein degradation in the rumen and increasing the flow of protein and essential amino acids to the intestine (Mc Nabb et al., 1996). Other benefits include reduced impact of intestinal nematodes and nematode larvae (Waghorn, 1996). However, higher concentrations of condensed tannins have detrimental effects on animal's performance (Pritchard et al., 1992). Tannin concentrations higher than 5% adversely affect forage intake and digestibility of Mediterranean shrubs, such as *Quercus calliprinos*, *P. lentiscus* (Perevolotsky et al., 1993) and *Ceratonia siliqua* (Silanikove et al., 1994, 1996). Condensed tannins bind and precipitate proteins in the rumen (Jones and Mangan, 1977), reduce protein degradation and reduce absorption of amino acids reaching the small intestine, resulting in low digestibility and voluntary intake.

Non-fiber carbohydrate levels (mean = 26.84%) were similar to ADL contents (mean = 24.27%). The samples of *Q. ilex* were collected in summer and had similar ADF and ADL but lower EE, CP, IVOMD and consequently lower NEL than reported by Poli et al. (1996) collected in a coastal Mediterranean environment from December to March 1990. The lower productivity and nutritive value of evergreens in summer is a general feature of the Mediterranean environment (Mooney, 1981; El Aich, 1991).

Shrubs had low OM digestibilities (36.17%) and NE values (3.49 MJ/kg DM), both generally associated with thick cell walls (Cutler et al., 1977), thick cuticle, high level of waxes, cutin, pigments, essential oils, highly lignified NDF, tannin and a low level of protein. Differences in IVOMD among shrubs (27–43%) were in the range of 20–61% as reported by Alibes and Tisserand (1990).

The P content in leaves and twigs decreased from June to December and were lowest during August, when Ca:P ratios reached 11.0 in leaves and 5.0 in twigs (El-Shatnawi and Turuk, 2002). Phosphorous in shrubs was low (0.06–0.1% in DM) in comparison with the required minimum of 0.20%, and P supplementation appears to be essential (McDowell et al., 1984; Breves and Schroder, 1991). Furthermore, high Ca:P ratios reduce absorption of phosphorus (NRC, 2001). Some (sub)Mediterranean parts of Croatia are noted for low P and Se concentrations in soils and plants, but more in-depth investigations are needed (Grbesa, 1996). Durand and Komisarczuk (1988) recommend available phosphorus should be at least 5 g/kg OM digested to optimize degradation of cell walls (NDF) by microbes.

Concentrations of calcium of >1% (Table 1) have been associated with lower DM intake, and excess Ca can interfere with trace mineral absorption (especially zinc) and lower performance of dairy cattle (NRC, 2001).

4.2. Variation in shrub intake and preference

The major finding of this study was that goats ate twice as much of most shrubs per unit of body weight as did sheep, even though both species have a long history of browsing on Mediterranean shrub ranges. The rank order of preference was similar for both goats and sheep even though the amount eaten was usually very different. Previous studies have also shown that goats often eat more of some shrubs than do sheep (Nefzaoui et al., 1993; Bartolomé et al., 1998). There are several possible explanations for this difference.

In many traditional systems in the Mediterranean Basin, sheep and goats are mixed feeders. However, under shrubland grazing systems goats consume a larger proportion of browse than sheep (Nefzaoui et al., 1993; Bartolomé et al., 1998). There are considerable differences in the utilization of the Mediterranean vegetation between local and introduced goats (Papanastasis and Liacas, 1991; Dziba et al., 2003).

In accordance with previous studies (Bartolomé et al., 1998; Leclerc, 1985; Bullock, 1985) goats selected more high fiber species (Table 3) than sheep. High lignin in goats' diets indicates that goats may have mechanisms to attenuate the undesirable effects of lignin (Howe et al., 1988). *Q. ilex* and *Erica arborea* also were highly preferred by goats. *Erica* was preferred among shrubs by both goats and sheep species in the study of Bartolomé et al. (1998), even it not only has the lowest IVOMD (Table 1), but also the lowest tannin concentration.

Goats in our study consistently ingested higher levels of all shrubs than did sheep, especially *P. lentiscus* and *J. phoeniceae*. These two shrubs were the least preferred, presumably not due to poor nutritional quality but because they contained high concentrations of secondary compounds. High tannins in *P. lentiscus* (Perevolotsky et al., 1993) and high level of essential oils and terpenes in *J. phoeniceae* (Pritz et al., 1996; Riddle et al., 1996) reduce preference of both shrubs by sheep and goats. Tannins also limit intake of strawberry trees (*A. unedo*) (Table 3), a species known for its aggressive regrowth after fire or cutting (Rogosic and Dumancic, 1996).

Use of the Mediterranean shrublands is often limited by secondary metabolites, which adversely affect forage intake. Most (80%) Mediterranean shrubs contain tannins (Rhoades, 1979) often at levels of 10% or more in DM (Levin, 1976). Seventy to 80% of a goats' diet in the Mediterranean woodland is composed of shrubs (Bourbouze and Rubino, 1992) characterized by moderate to high tannin levels (2–20%) (Silanikove et al., 1996). Goats appear to be more tolerant of tannins than sheep, in part because sheep lack salivary secretions containing proline-rich proteins, which bind tannins alleviating their aversive effects (Hoffman, 1987).

Sheep and goats do not differ in DM and OM digestibility when moderate- or good-quality forages are fed, but fiber digestibility of low-quality forages is greater in goats than sheep (Schmid et al., 1983; Doyle et al., 1984). The cell wall digestibility of some Mediterranean shrubs is 4–9% higher in goats than in sheep (Wilson, 1977). Likewise, Gordon and Illius (1992) reported that goats appear to digest more extensively plants containing toxins than sheep. Differences in utilization of toxin-containing shrubs may be partly a function of differential ruminal metabolism of toxins (Kronberg and Walker, 1993) or differential biotransformation of the absorbed toxins (Villalba et al., 2002).

Q. ilex, *E. multiflora* and *V. tinus* were more palatable to sheep and goats compared to the other three shrubs, although all of those shrubs contain some chemical compounds or physical defenses that are feeding deterrents to wild and domestic animals. Tannins in holly oak (*Q. ilex*; Table 1), the dominant species in the central Mediterranean ecosystem, are responsible for a marked reduction in digestibility and intake (Rogosic et al., unpublished). Iridoid glycosides and terpenoids in *V. tinus* (Tomassini et al., 1995) also limit intake by sheep and goats.

Several studies have reported on the influence of spinescent growth in shrubs on the feeding behavior of mammalian browsers (Cooper and Owen-Smith, 1986; Ortega-Reyes and Provenza, 1992). This study suggests that spines may have little influence in the preference for *Q. ilex* and *E. multiflora*. Both species contain spines, but in neither case did spines appear to deter feeding.

5. Conclusion

The dominant shrubs of the Mediterranean maquis – *Q. ilex*, *E. multiflora*, *A. unedo*, *J. phoeniceae*, *V. tinus*, *P. lentiscus* – are generally of low quality and contain secondary metabolites that adversely affect forage intake. While the rank order of preference was similar for goats and sheep, goats had markedly higher intakes than sheep of all shrubs except *Q. ilex*. Although physical and morphological deterrents may influence acceptability, chemical composition, digestibility and secondary metabolites were more important determinants of the preferences of sheep and goats. Goats are better suited to graze Mediterranean maquis in terms of potential shrub use.

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